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Seasonal habitat selection and ranging of domestic cats (*Felis catus*) in rural and urban environments

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Abstract

Domestic cats (*Felis catus*) thrive at high densities alongside humans in urban and rural environments and are responsible for excessive wildlife predation worldwide. As urbanisation and farmland expands, and domestic cats inevitably reach previously unoccupied habitats, management plans will rely on understanding cat ranging behaviours. Cat movements and habitat selection may differ depending on their surroundings, and consequently, we sought to assess how male and female cat behaviours varied during different seasons in urban, suburban, and rural environments. In cities and farmland in the UK, the location of 56 owned cats (26 F:30 M) was recorded every 5 min for a total of 5237 h using GPS collars (454 ± 25 fixes over c. 4 days per individual). Urban and rural cats exhibited similar patterns of home ranges, maximum distances travelled from their owner's house, and habitat selection, where they selected for built-up areas with good cover and avoided open spaces. Cats spent an average of 75% of their time outside their owners' house or garden and therefore had great potential to encounter wild prey. Males in rural areas were almost twice as active than other males but all exhibited crepuscular activity patterns compared to cathemeral or diurnal females. In summer, cats had smaller home ranges and were more nocturnal, poentially concentrating their impacts around core areas during hotter months. Similarities in cat ranging behaviours across the urban–rural gradient suggest management plans can be equally applied in areas alongside cities as well as farmland. Buffer or exclusion zones of 750 m around protected areas would exclude 95% of cats, but specialised management, such as periodic confinement during specific active periods, could prove effective during vulnerable prey species' breeding seasons. These findings improve our understanding of how cat ranging is affected by urbanisation under seasonal variation, and can be used to tailor management strategies as new species and populations are exposed to domestic cat predation.

Keywords Home range, Temporal activity, GPS, Management, Predation, Movement, Urbanisation

Background

Domestic cats (*Felis catus*, hereafter 'cats') are one of the most widely distributed mammals on earth, with an estimated 370 million living as pets worldwide [5]. They live alongside humans in small rural populations and in large cities where they can live at densities of up to 2500 cats per km^2 [1]. With cat distributions steadily expanding in parallel with human population growth, naïve prey populations and species are consequently being exposed to this generalist predator. Cats can have considerable negative

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impacts on wildlife through predation, disease spread, and interbreeding [25, 52], but variations in the environments where cats now persist, such as urbanisation level and season, may drive different behaviours, and understanding cat roaming is therefore crucial for developing effective management strategies. Domestic cats are cryptic by nature, but the development of lightweight biologgers provides an opportunity to study domestic cat behaviours in fine detail. These technologies faiclitate research into how the roaming behaviours of male and female cats differ across a rural to urban gradient in different seasons in the UK, and we discuss how the results can inform more effective management strategies, such as exclusion zones or confinement to their owners house.

The large population of domestic cats has a severe detrimental impact on small mammal, reptile, and particularly bird populations worldwide [24, 30, 34]. National appraisals of predation events often run into the hundreds of millions per year (see Trouwborst et al. [51] and refs therein), and cats have been responsible for at least 14% of the mammal, reptile, and bird extinctions globally [38]. Cats can also impact other predators, including by interbreeding with wildcat species, thereby diluting valuable genetics [28, 47]. Encounters with wildlife by cats will depend on their ranging behaviours, habitat use, and activity patterns.

Environmental and anthropogenic factors known to affect cat ranging behaviours include whether cats are owned or feral [21], their sex [19], neutered status [44], weather and the seasons [34, 52], and the degree of urbanisation [21]. There is however, little concensus on the affects of these factors. A high level of urbanisation can lead to smaller home ranges and while some studies have shown that cats use habitats in proportion to their availability, some select habitats that provide more cover, [9, 18–21]. Urbanisation can also affect prey selection and the timing of hunts; rural cats select predominantly rodent prey, whereas urban cats preferentially target bird species [25, 31]. Cats have also been found to hunt more frequently at night [50] but this needs to be researched further in different environments. Furthermore, human activity associated with urbanisation also effects cat diel activity patterns [2, 7, 43], where high densities of domestic cat populations elicit nocturnal activity rather than crepuscular movements [10].

The complexity of these interactions between environmental and anthropogenic factors are further compounded by biological factors. Male and female cats show pronounced sexual differences in home range size, with males regularly ranging further than females [14, 29, 46, 52](and see [19] for a meta-analysis). This is common among felid species, where males establish a large territory encompassing multiple females, however, high densities of cats in cities make this population structure near-impossible. No clear pattern in home range has been established in urban areas, and male and female cats can further have varying home ranges in different seasons [57], whereas others show consistency over time [20, 29]. Localised weather can also have extreme impacts with snowfall reducing cat home ranges by up to 94.5% [52]. These seasonal variabilities will also impact predation events, for example, 85% of hunts occurred in the warm season in the south eastern USA [34]. Season and sex have also been shown to impact the time of day that animals are active [3, 9, 15, 43, 56], with cathemeral, diurnal, crepuscular, and nocturnal patterns seen. Home ranges and diel activity patterns will therefore be a result of numerous driving factors, potentially including mating and territorial patrols (or latent drivers thereof in neutered animals). However, monitoring these trends is an imporant measure for managing cat predation as cats that maintain large home ranges and synchronise diel and seasonal activities with prey species will likely encounter more prey and increase hunting success.

To decrease the impacts of owned cats on wildlife, a number of different tactics can be employed including using individual bells and colourful collars [18, 53], increasing meat content in their diet [8], and raising awareness of owners about wildlife predation [11, 36]. Larger scale actions can also include confinement of cats indoors in certain areas [27, 32, 37] and setting up exclusion or buffer zones around vulnerable habitats, where cat ownership is limited or prohibited to decrease cat density [19, 50]. Given the inconsistent differences seen between cat ranging behaviours in urban and rural environments, control measures designed to affect ranging can be tailored to specific locations as well as seasons [12, 48, 49], including defining the distance of the buffer zone, or encouraging confinement for certain periods of time.

In the United Kingdom, the cat population now exceeds 10 million individuals and it has been estimated that over 92 million prey items are brought home by cats each summer, including at least 27 million birds and five million reptiles and amphibians [42, 54]. At least 44 wild bird species and 20 wild mammal species were predated, demonstrating the immense impact cats have on native species. With such a large cat population and high predation levels, the UK is an important location to investigate variation in cat ranging behaviour, particularly in Northern Ireland, where there is a number of Endangered and protected species that live in close proximity to farms and cities, including red squirrels (*Sciurus vulgaris*), the Irish stoat (*Mustela erminea Hibernica*), and various bat species (Chiroptera order). GPS loggers present an accurate and efficient method to monitor the movement and behaviours of free-ranging animals and provide detailed metrics that can be used to assess cat ranging [20, 41, 50]. We use them here to investigate whether cat home range, distances travelled, habitat use, and activity patterns were associated with level of urbanisation, season, and sex, and any interactions therein. This not only gives a more extensive understanding of cat ranging in the UK but can also be used to tailor management strategies, including predicting an effective size for exclusion zones for different urban areas and whether cat confinement at particular times of day or year might be most effective.

Materials and methods

Study area and animals

Cats were studied in a range of locations around Belfast, Northern Ireland. We enlisted the participation of cat owners from different areas including cities, towns, villages and farmhouses to ensure that we collected information from a variety of "urban", "suburban", and "rural" landscapes ([20, 31], see Additional file 1: Fig. S1). Participants were enlisted through author's networks, as well as word of mouth. The owner's house was visited to assess each cat's environment, which was categorised into urban, suburban, or rural based on the human population density, density of buildings, and habitat type (see [21, 44]). Urban areas consisted of dense residential housing that contained commercial and building works, with small gardens and limited green space. Suburban areas consisted of mostly detached or semi-detached housing with larger gardens and some countryside or nature areas nearby. Rural areas consisted of grassland, trees, farmsteads and farmland, with low human population densities (based on [44]). "Urbanisation" or "environment" here refer to the type of housing present, with urban areas presenting dense human populations in a city and rural areas denoting farm or villages. "Habitat" refers to the small patches and areas within a cat's home range, such as commercial buildings, grassland, or rivers (see below for each definition).

In total, 56 cats were collared; 30 males and 26 females. Data were collected from December 2016 to August 2017 which included three seasons; winter, spring, and summer (Additional file 1: Fig. S1 and Table S1), and all individuals were neutered or spayed except one male. The owners were asked about the cat's age and their most recent recorded weight. The mean age was 6.0 ± 4.1 years and the mean weight was 4.9 ± 1.0 kg. Each cat was monitored once for 4–5 days, during which time they were allowed free access to their owners' house and outdoors. Weather data were obtained from the Belfast meteorological office website [40]. Throughout the monitoring period, average daytime temperatures increased from winter to summer, and precipitation levels varied across the seasons, where rainfall in spring was one third of the amount that fell in both winter and summer. Average daylight hours varied between the seasons, increasing from around 9 h in winter to over 15 h in summer (Additional file 1: Table S2).

GPS data collection

Initially cats were fitted with 'dummy' collars, which were deployed on days 1 and 2 of the monitoring period. They consisted of a standard cat collar with a small weighted box that were the same size and weight as the functioning collars, and allowed the cat to become accustomed to wearing a collar as well as the weight of the device. The GPS collars were then fitted and provided approximately four to five full days of continuous data per individual. Collars were equipped with a GPS device (i-gotU USB GPS Travel & Sports Logger—GT-120, Mobile Action) and a VHF transmitter (Tabcat homing tag © 2016 Loc8tor Ltd.). GPS devices were set to record positional fixes every 5 min. The weight of the collar and devices was 61 g, which was less than 1.3% of the average cats' body mass. Quick-release collars, that could detach easily (Breakaway buckle collar, Rogz Ltd. 2002/030628/07), were used throughout to prevent injury or entrapment. During the deployment, two collars did become detached, but if this occurred cats were fitted with replacement collars on the same day. Detached collars were then found using the VHF transmitter. A total of 93.52 ± 12.56 h of GPS data were recorded per individual.

GPS data analysis

GPS files were downloaded using the manufacturer's software (@Trip version 5.0 Build 1612.2045). Any positional fixes that were recorded when the collar was not attached to the cat were removed as were any errant points [6]. Errant points were defined as consecutive GPS coordinates recorded over 1 km apart within the 5-min period [6]. The parameters below detailing the cats' movements were calculated from the GPS data using QGIS (version 2.18.7, 2016) and R (version 3.4.0, 2017).

Home range areas were calculated for each individual as the 100% minimum convex polygon (MCP) [21, 50]. We did not include 95% or 50% MCP home ranges as the cats spent most of their time in their owners' house and garden so this metric was not informative for habitat use outside this core area. MCP was calculated as there would likely be an underestimation for, for example, kernel density home range estimates, given a small effective sample size per individual (i.e., non-autocorrelated daily fixes = ~4 per cat, see Silva et a. 2021). The MCP home range was also used in further analysis to asses all habitats that the cats could have accessed.

The available habitats were identified according to Horn et al. [21] for the area encompassed by the home range. Horn et al. [21] studied cats in urban and rural locations in the USA and used satellite imagery to identify the habitats. The habitats in our study were identified according to their categories:

a) Farmland: Crop fields and ploughed land
b) Improved Grassland: Agricultural grazing fields, sports fields, parks
c) Trees: Trees, hedgerows, woodland, including urban trees
d) Rivers: Rivers and streams

Anthropogenic structures were categorised [22] as

e) The owners' house: including the garden
f) Private housing: Residential housing and gardens
g) Commercial: Commercial and industrial areas, including but not limited to shops, schools, and construction sites
h) Farmstead: Farm buildings, sheds, barns, and yards
i) Roads: Roads, pathways, footpaths.

The area of each habitat was measured by superimposing the 100 % MCP home range outer limit onto Google satellite imagery and manually outlining the distinct habitats within it. The area was measured to the nearest square meter using polygon area analysis (QGIS version 2.18.7, 2016, 'polygon' and 'area' tools). Each habitat was recorded as a percentage of the individual cats' home range area, to allow comparisons between individuals, and between environments. This was termed the "*habitat available*" to each cat, and we could then calculate the amount of time spent in each habitat, which was termed the "*habitat use*" [21, 22].

Each cat's habitat use was calculated as the number of GPS points that fell within each habitat. This was used to determine the amount of time the cat spent in a particular habitat, as a proportion of the total GPS points recorded. The Jacobs' index [22] (Eq. 1) was used to assess whether the cat's habitat use was in proportion to the availability of that habitat or whether certain habitats within a cat's home range were preferred or avoided. Jacobs' index uses habitat availability and habitat use to calculate proportional use and was used to describe each cats' habitat selection:

$$Jacobs'\ Index = \frac{(r-p)}{(r+p-2rp)} \tag{1}$$

where r is the proportion of GPS points in a habitat, and p is the proportion of the home range consisting of that habitat [22]. The results of Jacobs' index scale between 1 and -1 for each habitat. A '0' result would indicate that the cat used the habitat in direct proportion with habitat availability. Positive values show that the cat spent proportionally more time in a habitat, whereas negative values indicate proportionally less time spent in the habitat. GPS points within the owners' house and garden and the measured area (in m^2) of this were initially included but then removed for habitat selection analysis because of the high preference for this area which skewed the data and gave a negative bias to all other habitats [13, 21]. The habitat availability and habitat use data presented here only therefore present behaviour which is outside of the 'owners' house and garden' environment, and the proportion of habitat availability and use was calculated as a proportion of area or GPS points having removed 'owners' house and garden' data.

The maximum linear distance travelled (MLD) was calculated as the distance to the furthest GPS point that an individual travelled from its owner's house [32, 39, 41]. The 'furthest point' method can overestimate the ranging behaviours of the cat if the animal goes on one long foray but does not regularly stray far from home [50], but here, these may represent hunting excursions and are of interest for management practices.

The activity level of the cats, measured as mean speed, was calculated as the sum of the distance between consecutive GPS fixes for the whole measurement period, divided by the length of time the cat was monitored (in hours). This was calculated to assess how active the cats were during the collaring period with the implication that there may be differences between seasons or environmental activity not reflected by changes to home ranges or MLD.

The temporal pattern of activity was calculated as the distance between consecutive GPS coordinate fixes (calculated using software @TRIP version 5.0 Build 1612.2045) that was summed between each hourly period (00:00–00:59, 01:00–01:59, 02:00–02:59, etc., [9, 43]). Temporal activity was calculated as the average for each hour (e.g., at 02:00–02:59) for 4 days of monitoring. Temporal activity patterns of each individual were analysed to investigate what hours cats were most active, and assess whether this was related to urbanisation level, season, or sex.

Statistical analyses

Statistical analyses were conducted using R (version 3.4.0, R core team 2014). The results, unless otherwise indicated, are expressed as mean ± 1 standard error. All response and explanatory variables of general linear models are detailed in Additional file 1: Table S3. Models were generated to test specific hypotheses and all model residuals were examined for normality using QQplots. R^2 was determined using the *MuMIn* package [4].

General linear models (GLM) were used to examine whether there were any effects of the explanatory variables on the response variable of the cats' home ranges, mean distance travelled (MDT), maximum linear distance (MLD), and the percent time the cat spent at the owner's house and garden. The explanatory variables used in separate models included either an interaction between environment and season, environment and sex or season and sex. The small sample size precluded assessment of three-way interactions. Where no significant interaction occurred, environment, sex, or season were included as lone explanatory variables. Home ranges were also modelled against age or mass. Home ranges for the cats were log-transformed prior to analyses to achieve normal distribution of the model residuals. After including all cats in the analysis, post-hoc GLM analyses were undertaken to investigate how different groups were affected by the explanatory variable, for example, cats were split according to whether they lived in urban, suburban or rural environments, and GLM models were used to test the effects of the season within this group.

General linear models were used to examine whether the area of the owner's house and garden differed with the environment (i.e., were rural houses and gardens larger than urban houses), and also whether the area of the owner's house and garden differed with the environment, as a percent of the cat's home range.

One-sample *t* tests were used to determine whether the Jacobs' index result was significantly different from the expected '0' value of opportunistic use with no habitat preferred, giving three definable habitat selection classifications: Preferred (significantly positive), opportunistic (not significant from 0), or avoided (significantly negative) [35, 45].

Generalised additive mixed models (GAMMs) were generated using the *mgcv* R package [55] and were selected to determine whether the cat's mean distance travelled each hour varied with the time of day by testing for a significant interaction between the smoothed time of day and the environment, season, or sex. A k of 6 and a cyclic cubic regression spline were used in all GAMMs to smooth over 6 h and to denote the cyclic pattern of each day. Cat ID was included as a random variable in all GAMMs due to multiple measures of the mean distance travelled for each hour for each cat.

GAMM models were then selected to test our hypotheses about the interactive effects of environment, season or sex on temporal activity. Cats were grouped by environment and we included season or sex as the explanatory variable (e.g., to assess whether males and females differed in temporal activity in urban areas). Similarly, cats were grouped by season and we included environment or sex as the explanatory variable (e.g., to assess whether males and females differed in temporal activity in summer). Finally, environment or season was included as explanatory variables to examine differences between male and female cat activity. Small sample sizes precluded the inclusion of interactions between explanatory variables as some "groups" (i.e., males in suburban environments in spring) had too few individuals (range: 0–7, see Additional file 1: Table S1).

Results

A total of 5237 h of GPS data were collected (93.52 ± 12.56 h per individual). On average, 453.50 ± 25.15 GPS fixes (range: 86–911) were recorded per cat.

Home range

The mean home range of cats was 8.63 ± 0.95 ha (min: 0.63 ha, max: 30.87 ha). The cats' home range size did not vary between environments ($F_{(2,53)} = 2.43$, $p = 0.10$) or between sexes ($F_{(1,54)} = 0.69$, $p = 0.41$). There was an effect of season on home range ($F_{(2,53)} = 6.10$, $p < 0.01$), with cats in summer (5.38 ± 1.22 ha) having smaller home ranges than in winter (9.61 ± 1.45 ha) or spring (11.30 ± 2.13 ha). This was maintained for both male and female cats (male: $F_{(2,24)} = 3.40$, $p = 0.050$; female: $F_{(2,26)} = 3.53$, $p < 0.05$) (Fig. 1B), and male and female cats had similar home range sizes in each season (winter: $F_{(1,20)} = 0.14$, p = 0.71, spring: $F_{(1,13)} = 0.69$, p = 0.42, summer: $F_{(1,17)} = 1.64$, p = 0.22, Fig. 1A).

Habitat use

Cats spent a substantial proportion of time within their owners' house and garden. This habitat was highly preferred, with a Jacobs' index of 0.92 ± 0.01. On average, 24.66 ± 2.25% of GPS points occurred in cats' owners' house and garden, despite this habitat only accounting for 1.11 ± 0.12% of their home range area. Sex nor season affected the amount of time cats spent in and around their owner's house ($F_{(1,54)} = 1.60$, $p = 0.21$; $F_{(2,53)} = 2.82$, $p = 0.07$ respectively) but urbanisation level did ($F_{(2,53)} = 8.91$, $p < 0.001$). Post-hoc analysis revealed that this was true for females ($F_{(2,26)} = 7.82$, $p < 0.01$) but not for males ($F_{(2,24)} = 1.71$, $p = 0.20$); urban females spent 9.90 ± 5.79% of their time in the house and garden, compared to suburban females (26.30 ± 14.76%), and rural females (40.05 ± 17.57%; Fig. 2A). The area of rural and suburban cats' house and garden habitat were 3.91 and 1.97 times larger than those of urban cats', respectively.

When outside their owners' house, cats preferred to stay within private housing and farmsteads ($t_{(54)} = 4.08$, $p < 0.001$; $t_{(16)} = 2.33$, $p < 0.05$), whereas they strongly avoided commercial areas ($t_{(30)} = -5.64$, $p < 0.001$).

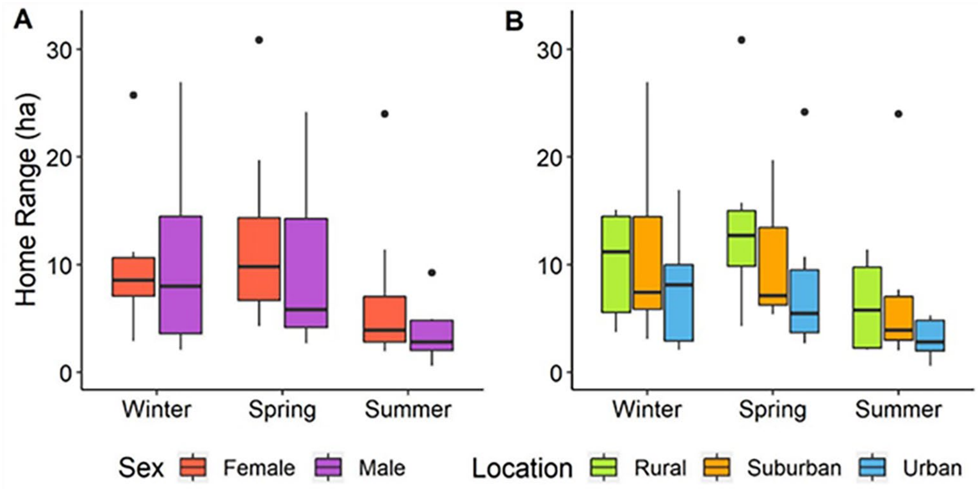

Fig. 1 Home range area (ha, hectares) of cats grouped by sex (**A** males: red, and females: purple), and environment (**B** rural: green, suburban: orange, and urban: blue)

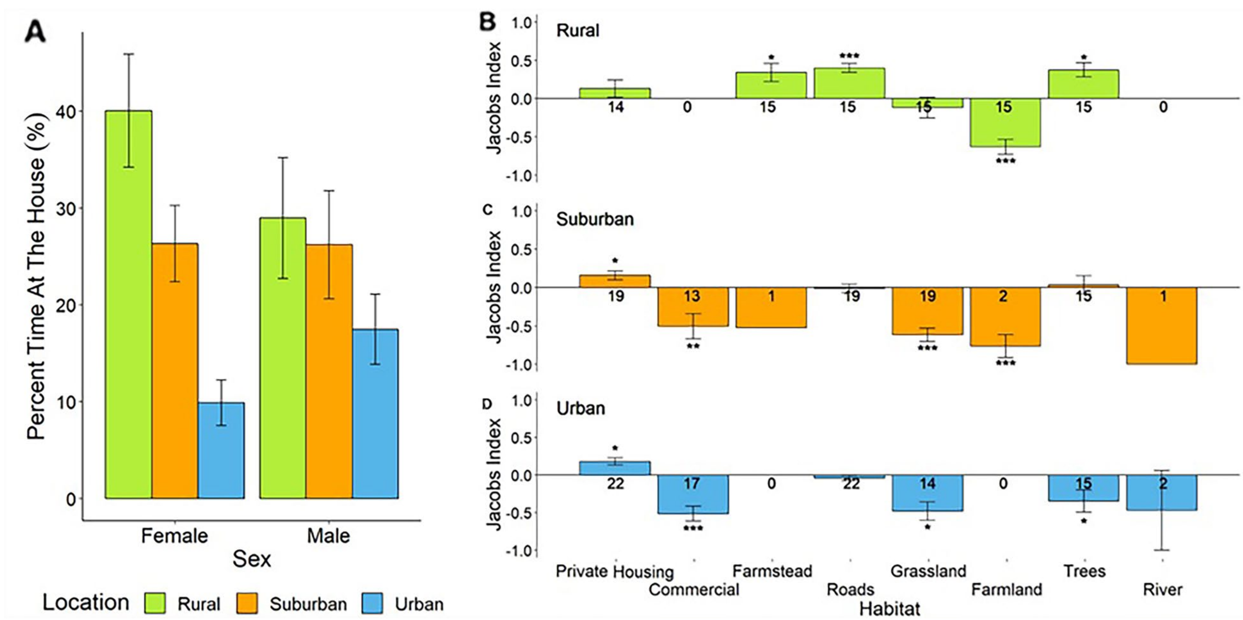

Fig. 2 **A** Percent of time male and female domestic cats spent at their owners' house and garden, grouped by environment: rural (green), suburban (orange), and urban (blue). **B**–**D** Jacobs' index results for cat habitat preference when the cat is outside its owners' house and garden. Error bars denote standard errors. Numbers indicate how many cats encountered each habitat. Asterisks indicate whether the result is significantly different to a null Jacobs' index of 0 ($p < 0.05$ = "*", $p < 0.01$ = "**", $p < 0.001$ = "***"). Positive significant results indicate a preferred habitat, non-significant results indicate a habitat used opportunistically, and negative significant results indicate a habitat that is avoided

Urban and suburban cats showed preference for private housing ($t_{(21)} = 3.64$, $p = 0 < 0.01$; $t_{(18)} = 2.74$, $p < 0.05$), whereas rural cats did not prefer or avoid it ($t_{(13)} = 1.172$, $p = 0.26$) (Fig. 2B–D), but rural cats also had access to, and preferred, farmstead buildings ($t_{(14)} = 2.10$, $p < 0.05$). Rural cats also used roads selectively ($t_{(14)} = 6.95$, $p < 0.001$), whereas urban and suburban cats did not ($t_{(21)} = -1.11$, $p = 0.28$; $t_{(18)} = -0.25$, $p = 0.81$).

All cats avoided open grassland ($t_{(47)} = -5.92$, $p < 0.001$) and when analysed further, urban and suburban cats significantly avoided it ($t_{(13)} = -1.88$, $p < 0.01$; $t_{(18)} = -7.06$, $p < 0.001$), rural cats used it opportunistically ($t_{(15)} = -0.87$, $p = 0.40$). Farmland was significantly avoided ($t_{(17)} = -6.72$, $p < 0.001$), particularly by rural cats ($t_{(14)} = -6.38$, $p < 0.001$), but it was only encountered by two suburban cats, and no urban cats. Rural cats utilised trees and hedgerows preferentially ($t_{(14)} = 4.01$, $p < 0.01$) and suburban cats used them opportunistically ($t_{(14)} = 0.28$, $p = 0.79$), whereas urban cats avoided using this habitat ($t_{(14)} = -2.34$, $p < 0.05$) (Fig. 2B–D).

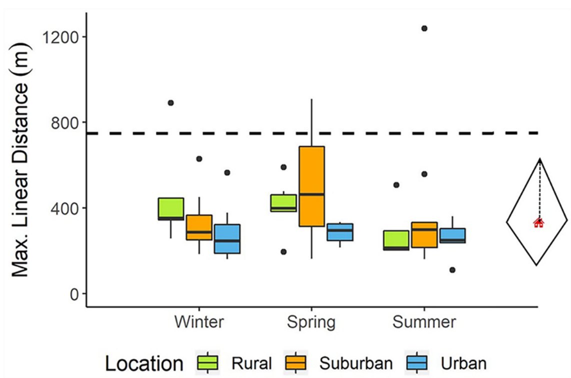

Fig. 3 Maximum linear distance (m) the cats travelled from their owner's house in each season, grouped by environment: rural (green), suburban (orange), and urban (blue). 95% of cats did not travel further than 750 m from their owner's house (horizontal dashed line)

Distances travelled

The maximum distance that a cat was recorded to travel from their owners' house was 1239 m, and 95% of cats did not roam further than 750 m (Fig. 3). There was no difference in the MLD travelled in different environments ($F_{(2,53)} = 2.57$, $p = 0.086$), in different seasons ($F_{(2,53)} = 0.27$, $p = 0.77$), or between sexes ($F_{(1,54)} = 0.55$, $p = 0.46$) and no interactions between the three variables. The cats travelled an average of 151.18 ± 7.71 m per hour. Their mean speed did not vary with season ($F_{(2,53)} = 0.81$, $p = 0.45$) or sex ($F_{(1,54)} = 0.073$, $p = 0.79$), but was affected by environment ($F_{(2,53)} = 3.77$, $p < 0.05$). Rural males had faster speeds (212.77 ± 27.25 m) than both suburban (137.79 ± 16.60 m) and urban males (127.61 ± 13.43 m). In rural areas only, males travelled faster than females ($F_{(1,13)} = 4.94$, $p < 0.05$).

Diel activity

Cats exhibited crepuscular activity patterns (peaks at sunrise ~ 06:00, and a maximum value at sunset ~ 19:00, Fig. 4). Male and female cats were active at different times of day ($F_{(4)} = 11.79$, $p < 0.001$) with the crepuscular pattern driven exclusively by male cats. This trend continued with differences in activity patterns of males and females in winter ($F_{(4)} = 7.94$, $p < 0.001$) and spring ($F_{(4)} = 6.93$, $p < 0.001$), when males were crepuscular and females were more diurnal or showed little variation throughout the day. In summer, cat's activity became more nocturnal

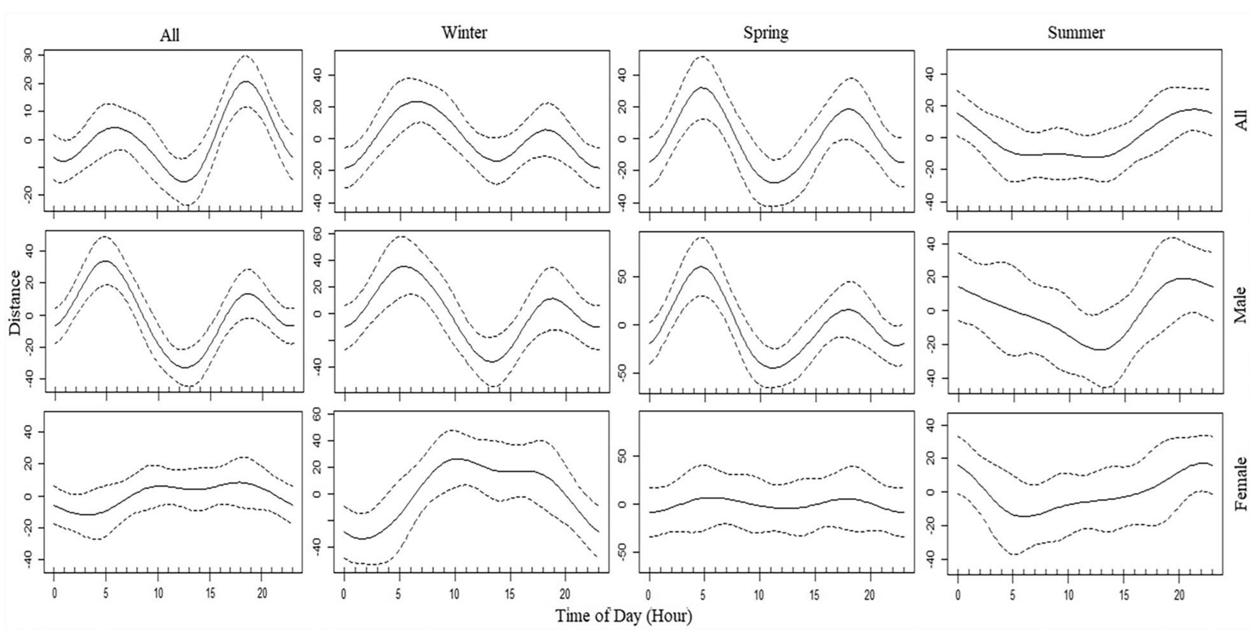

Fig. 4 Domestic cat temporal activity in winter, spring, and summer. Data displayed shows the GAMM transformed function of time and distance, with an interaction with season (All), and with an interaction with sex modelled separately for each season (Male and Female). Cat ID was included as a random factor. Dashed lines represent 95% confidence intervals

and male and female cats displayed similar activity patterns ($F_{(4)} = 1.64$, $p = 0.16$).

Urbanisation level also affected cat activity patterns, where suburban cats differed to urban ($F_{(4)} = 6.61$, $p < 0.001$) and rural cats ($F_{(4)} = 5.96$, $p < 0.001$) and had periods of high activity around late morning and midnight. While both urban and rural cats exhibited crepuscular activity patterns, they also differed ($F_{(4)} = 5.75$, $p < 0.001$) as urban cats had a higher peak of activity around sunrise and rural cats were most active around sunset. Rural females exhibited a predominantly diurnal activity pattern with a peak of activity around sunset, driving this trend.

Discussion

Domestic cats predate millions of birds and mammals each year worldwide, which increases as human populations, urbanisation and farmland expands into new areas with naïve prey populations [5, 42]). Management plans will be crucial to help protect vulnerable habitats and species, including those in Northern Ireland such as the native red squirrel, pine martens, and vulnerable bat species. Exclusion zones and confinement of cats have been widely proposed as potential strategies to reduce cat predation, and in this study, we assessed how urbanisation level, season, and sex affected cat ranging behaviours and therefore how management plans may be tailored to maximise effectiveness.

We tracked 56 domestic cats' locations across multiple seasons and varying levels of urbanisation in Northern Ireland. Similar core home range sizes were documented across all urbanisation levels and seasons, and for cats of all sexes, ages and weight. This finding aligns with previous research showing that domestic cats tend to establish a home range centered around their owner's property [19, 20]. We expected to find that males had larger home ranges than females [19, 26], but Metsers et al. [41] also found similarities between male and female cat home ranges in New Zealand and that they caught similar numbers of prey. However, they also found that home ranges were constrained in urban areas by high cat densities, a trend not found in our study. It is possible that the cats in this study would have larger home ranges if they were monitored over a longer period, Kays et al. [26] found that home range variance decreased after 5 days of GPS collaring and were most precise at 10 days (with a 20% larger home range at 10 than at 5 days), but the battery life of the collars constrained the deployment period to 4 days used here. In contrast to other studies, we did however deploy "dummy collars" for 2 days prior to GPS deployment to reduce any effect of the collars on the data recorded for cat ranging behaviours.

Cats exhibited smaller home ranges in the summer, suggesting they roam smaller distances from their core area during these months with hotter temperatures. This seasonal variation could have implications for wildlife predation, as cats may have a more concentrated impact during the seasons when their home ranges are smaller, potentially due to more abundant prey, reducing the necessity of large home ranges. Loyd et al. [34] found that 85% of hunts occurred in the warmer seasons, suggesting predation is highest in these core areas. Alternatively, cats may also be less likely to roam into wild landscapes, potentially decreasing predation of wild animals that live at the edges of urban or farmland areas. If we assume the cat population in an area is relative stable year-round, and that home ranges are non-exclusive, the number of days a cat is active outside will not vary but the risk of predation would shift from near owner's homes in summer to further into wild landscapes in winter and spring when home ranges are largest and there is the greatest potential to bring them into conflict with vulnerable young or nesting animals. Seasonal home range fluctuations and excursions outside the domestic cats' normal home range is an important factor to consider for domestic cat management in areas close to vulnerable habitats, such as woodlands with red squirrel populations or, further afield, wildcat habitat, as long range excursions are suggested to be the interspecific meeting points for the European wildcat (*Felis silvestris silvestris*) in France that may lead to hybridisation [16]. Future studies could benefit from the development of smaller loggers, particularly animal-borne video cameras [34], that could provide data on the mechanisms driving seasonal home range fluctuations and whether predation or another factor such as searching for a mate may drive variations.

Cats showed strong habitat preferences, and spent 25% of their time in and around their owners' houses and gardens on average, despite these habitats representing just over one percent of their home range. This likely represents a strong tendency to stay in areas where they are fed—all cats were provided regular meals by their owners, and shows a strong selection for abundant resources and security. Similarly, Kays et al. [26] also found remarkably small home ranges surrounding cat owner's housing. While we found that female cats in rural areas spent four times the amount of time (40.05%) at their owner's house and garden compared to female cats in urban areas (9.0%), rural house and gardens were also 3.9 times larger than urban house and gardens, suggesting that they may use the space around a central point uniformly, despite man-made delineations of an owner's house and garden. This trend did not however hold for males that spent a similar amount of time at home regardless of urban or rural environments. The high density of cats in urban areas may be driving the more territorial males to spend more time in their owner's house and garden to avoid conflict, whereas female cats, that are usually less territorial, spent more time outside their owner's house and garden in urban areas. For both males and females, the strong selection of their owners' house and garden emphasises the risk these cats pose to garden birds and mammals in both urban and rural environments.

Cats spent 75% of their time outside their owner's house or garden, indicating a high degree of risk posed to small animals in surrounding areas. The habitats selected by cats during this time did however vary based on their environment. Most cats showed strong preferences for private housing and farm buildings that provided ample cover, but rural cats preferred farmstead buildings and used roads more frequently than urban cats. This indicates that rural environments offer different opportunities and resources for cats, potentially affecting their ranging behaviours but also indicating that rural roads are not a barrier to rural cat roaming. They may even serve as easy travel routes as is often seen in wild felids that preferentially use trails [17]. Open grassland and farmland, however, was consistently avoided by cats. There may be an increased risk involved with open spaces from other predators such as foxes and raptors. These open habitats may present a natural barrier to domestic cat roaming if they are unwilling to cross it, but may also avoid the open areas due to a lack of cover when hunting [21]. The cats in this study selectively used treelines and hedges in rural areas that commonly indicate habitat edges, known for increased rodents and birds. These findings show that all cats are selective in their habitat use depending on the environment they are in, which has implications for prey species and management strategies in different habitats.

Exclusion zones can be used to decrease the impact of cats on specific key habitats or wildlife populations by preventing their habitation in nearby areas, and therefore decreasing predation pressure [52]. There is, however, little consensus on the width of the zone needed to prevent cats accessing vulnerable areas. In Australia, Metsers et al. [41] and Lilith et al. [32] suggest buffer zone widths of 2.4 km and 300 m, respectively. Kays et al. [26] also found that just 0.3% of cats roamed more than 1 km from their house. We would suggest an exclusion zone should be at least 750 m wide, which would prevent 95% of our cats from reaching protected areas. Furthermore, as cats avoid open green spaces, exclusion zones that are comprised of these may be most effective.

An alternative to exclusion zones is the confinement of cats to their owner's house. Confinement prevents hunting by removing the predator from the system [33], however, many owners do not want to continuously confine cats [18, 37] often citing concerns for cat welfare [23]. Selective and targeted confinement may increase owners' uptake of these policies as it would not be a permanent restriction on cat movements and therefore maintains cat welfare. Periodic confinement may help conserve populations of vulnerable species by, for example, preventing cats hunting during prey breeding seasons, when caring for young, or during peak activity times of specific species (e.g., bats leaving a roost). All the cats in this study were more nocturnal in summer which corresponds with other studies that found that 94% of hunts occurred at night [48], so confinement during this period may further limit predation. Further research would need to be conducted on whether shorter, hourly or daily confinement may decrease cat predation events or simply shift predation to another time. Furthermore, confining cats in areas where they are naturally more active may decrease predation; rural males were more active than suburban and urban males, which suggest that they may traverse longer routes and potentially have a wider impact on wildlife populations. Limited and specific confinement for short periods and for particularly active individuals or groups may reduce owner opposition to this method of cat management.

Conclusion

The findings of this study provide valuable insights into the ranging behaviours of domestic cats in various urbanisation levels and seasons. As human urbanisation increases and naïve populations are exposed to cat predation, management of hunting behaviours will become increasingly important. Consistent cat home ranges and habitat use in urban and rural areas suggest management plans can be developed based on trends across the study location. Our study found that buffer zones of 750 m around protected areas could exclude 95% of cats, and tailored strategies, such as confinement at night in summer, may protect vulnerable species during breeding seasons. These findings contribute to development of effective management strategies, aiding in the protection of wildlife that will increasingly encounter domestic cats.

Abbreviations

GLM General linear model
GAMM General additive mixed model
MCP Minimum convex polygon

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s40317-024-00367-0.

Additional file 1. The additional file provides further details on the methodology including on collar deployments and statistics. Further tables and figures are also presented.

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Author contributions
Carolyn Dunford: conceptualization, methodology, formal analysis, investigation, validation, data curation, writing—original draft, visualization, project administration. Sophie Loca: formal analysis, investigation, data curation, writing—review and editing. Nikki Marks: conceptualization, methodology, writing—review and editing, supervision, funding acquisition. Michael Scantlebury: conceptualization, methodology, resources, writing—review and editing, supervision, project administration, and funding acquisition.

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Availability of data and materials
The data sets used and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate
The study was approved by the Queen's University Belfast biological sciences ethics review board (code: QUB-BS-AREC-19-005).

Consent for publication
Not applicable.

Competing interests
The authors declare no competing interest.

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